MATING FREQUENCY IN *SCHIZOCOSA OCREATA* (HENTZ) WOLF SPIDERS: EVIDENCE FOR A MATING SYSTEM WITH FEMALE MONANDRY AND MALE POLYGYNY

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ABSTRACT. Courtship behavior has been studied extensively in the wolf spider *Schizocosa ocreata* (Hentz) (Araneae, Lycosidae). While much research has tested predictions of sexual selection theory regarding male traits and female mate choice, some critical assumptions about female behavior remain untested. To determine if females mate more than once, and to what degree copulation influences subsequent female mating, a multiple mating experiment was conducted. Virgin females were paired randomly with males in laboratory containers. If mating occurred, females were paired with a second male within 24 hr, after 3 days, or after 30 days (enough time for an egg sac to be produced). Of the 101 females tested, 83 (82%) mated with the first male they encountered. The probability of a female mating the first time was not influenced by female size, male size, or male age, but varied significantly with female age post-maturity. Of the 18 males that failed to mate, 3 were cannibalized. Of the 83 males that did mate, 12 were cannibalized after mating. There was no difference between re-mating treatments (1 d, 3 d and 30 d), and analysis of pooled data showed a highly significant difference in the proportion of virgin and mated females accepting males; most females mated only once (93%). In contrast, males appeared to court and attempt mating with every female encountered (virgin and mated), and a majority of males paired with more than one virgin female mated more than once (64.5%). Results suggest that female *S. ocreata* are essentially monandrous, while males are polygynous, and are discussed in the context of potential conflicts-of-interest between the sexes.

Keywords: Lycosidae, *Schizocosa*, mating systems, monandry, polgyny

Female mate choice may be expected to vary depending on the mating system of the species (Arnold 1994; Arnold & Duvall 1994; Lorch 2002). Spider mating systems, like all mating systems, are constrained by several factors: (1) whether males are able to mate multiply; (2) whether females will mate with more than one male; and (3) the nature of sperm storage and fertilization (Austad 1984; Eberhard 1985, 1996; Elgar 1998). Numerous studies suggest that the evolution of male and female mating behavior (male competition, mate guarding, cohabitation, multiple mating) may be influenced by sperm precedence patterns arising from the morphology of the reproductive tract of the female (Austad 1984; Eberhard 1985), although recent studies have revealed exceptions (Eberhard et al. 1993; Watson 1993; Eberhard & Cordero 1995; Elgar 1998; Uhl 1994, 1998; Schaefer & Uhl 2002). Studies of linyphiid spiders, for example,

demonstrate that most females mate more than once and multiple paternity broods are common (Martyniuk & Jaenicke 1982; Austad 1982; Watson 1990, 1991a, b). While many studies have shown varying degrees of polygyny and polyandry in spiders (Austad 1984; Eberhard 1985, 1996; Elgar 1998), Singer & Riechert (1995) found a primarily monogamous mating system in a desert agelenid spider, as a consequence of high travel costs to males and a significant decline in female receptivity after the first mating.

The mating strategies and courtship communication of jumping spiders and wolf spiders have been studied extensively (see reviews in Richman 1982; Richman & Jackson 1992; Jackson & Pollard 1997; Hebets & Uetz 1999, 2000; Uetz 2000; Uetz & Roberts 2002). Male salticids and lycosids often perform elaborate visual and/or vibratory courtship displays to elicit female receptivity, and male color patterns, leg decorations and vibration displays often serve as condition-in-

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dicating traits subject to female mate choice (Jackson 1980, 1981, 1986; Clark & Uetz 1992, 1993; Mappes et al. 1996; Parri et al. 1997; Kotiaho et al. 1998; Uetz 2000). The courtship behaviors of wolf spiders in the genus *Schizocosa* have been studied in detail (Mongomery 1903; Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983, 1986; Stratton 1997; Miller et al. 1998; Hebets & Uetz 1999, 2000). Males within this genus display considerable variation in foreleg ornamentation as well as courtship communication, and there is evidence of co-evolution between male signals and female sensory design (Hebets & Uetz 1999, 2000).

Male courtship behavior and female mate choice have been studied extensively in the brush-legged wolf spider *Schizocosa ocreata* (Hentz 1844) (see reviews in Uetz 2000; Uetz & Roberts 2002). Several studies have focused on visual cues provided by the presence of male foreleg tufts in this species, and their role in female mate recognition and preference (Scheffer et al. 1996; Uetz et al. 1996; McClintock & Uetz 1996). The role of tufts in male-male competition is unclear, as studies have produced mixed results. One study has shown that both naturally-occuring and experimental asymmetry in tufts affects the outcome of male-male contests (Uetz et al. 1996), while another study of males competing for females (triad mating experiments) has demonstrated that removal of tufts has no influence on mating success (Scheffer et al. 1996). Other studies suggest that tufts and leg waving displays may exploit a pre-existing sensory bias of female *Schizocosa* (McClintock & Uetz 1996), or serve as amplifiers (Hasson 1989, 1991; Taylor et al. 2000) of condition-indicating male behaviors or traits (Hebets & Uetz 2000). Recent studies have suggested that the relative size of male tufts may serve as a condition-indicating trait (Uetz et al. 2002).

Despite intense interest in sexual selection and especially female mate preference in lycosids, much empirical work has focused on male traits; i.e., differences in expression and the mating advantages of males with increased ornamentation via female mate choice (Hebets & Uetz 2000; Uetz et al. 2002). Perhaps because attention has been focused more on male traits and less on female preference, some critical assumptions regarding reproduc-

tive behavior in this lycosid model system remain untested. For example, while often assumed, it is currently unknown whether female *S. ocreata* mate with more than one male. Given high densities and a high rate of male-female encounter in the field (Aspey 1976; Cady 1984) as well as the presence of elaborate male secondary sexual characteristics (and their role in mate choice), theory would predict a promiscuous mating system in this species (i.e., both males and females mate multiply). In this study, we address this gap in our knowledge and test this hypothesis by conducting experiments to investigate whether female *S. ocreata* mate with more than one male and what variables affect female reproductive behavior.

METHODS

Immature *Schizocosa ocreata* were collected from the Cincinnati Nature Center Rowe Woods site (N39°09.904'; W84°15.377') in Clermont County Ohio, through April and May 2000. Spiders were brought back to the lab and housed individually under identical, controlled conditions (13hrs:11hrs light/dark cycle, temperature 23–25 °C and stable humidity). Spiders were raised to maturity in individual opaque plastic deli dish containers (11.5 cm diameter, 6.2 cm height). Constant moisture was provided via a cotton dental wick inserted through a hole on the bottom of the container and immersed in a dish of water below. Spiders were fed 2–3 subadult crickets (*Acheta domestica* L.) twice a week. Daily checks for molting determined the exact date of maturity, which was recorded for every spider.

To determine if females mate more than once, and to what degree copulation influences subsequent female mating, a multiple mating experiment was conducted. Virgin females ($n = 101$) were paired randomly with males, and if mating occurred, females were assigned to one of three re-mating treatments: (1) paired within 24 hr; (2) paired after 3 days; (3) paired after approx. 30 days (by which time 50% of females had produced egg sacs). These time intervals were chosen to account for a high rate of male-female encounter in the field (and the possibility of refractory periods in female propensity to re-mate), and/or the possibility that females may re-mate to obtain sperm for a second egg sac. If females

produced egg sacs, these were taken away before any re-mating attempt. Females that did not mate with the first male encountered were paired the next day with a different male. If a female did not mate after three pairings, that female was excluded from the experiment. Females were placed individually in a plastic box with filter paper lining the bottom (12cm x 17cm floor x 5cm walls) for one hour, after which a male was introduced. This allowed the females to acclimate and lay down silk and/or pheromones prior to the introduction of a male. All pairings were videotaped from above. While pairings were random, approximately one-third of males ($n = 31$) were paired with more than one female to test for multiple mating by males.

Data were analyzed using a contingency test with re-mating treatment (1 d, 3 d and 30 d) as the factor, and mating outcomes (mated once, mated twice) as the response, to determine if mating a second time was dependent on the mating treatment. These data were then analyzed using a McNemar's chi-square test for significance of changes, which is appropriate for paired samples (Zar 1999). Specifically, we tested the null hypothesis that the proportion of females mating with a second male is the same as the proportion of virgin females that mate with the first male they are paired with.

At the end of the experimental studies, spiders were humanely sacrificed using CO_2 anesthesia and preserved in 70% ethanol. After preservation, all individuals were digitally photographed with a Pixera 1.2 mega-pixel digital camera through a Wild M5 microscope. Measurements of individuals were then taken using the UTHSCSA ImageTool program (developed at the University of Texas Health Science Center at San Antonio, Texas and available from http://www.maxrad6.uthscsa.edu). Prosoma width, a widely used measure of body size, was determined for both males and females. Male tuft area and leg length were also measured. All egg sacs produced were preserved in 70% ethanol and dissected open using fine point scissors. All eggs were counted under a dissecting microscope (Wild M5).

The data set consisted of the following individual and pairing variables; age at time of pairings, whether the female ate the first male after mating, size measurements (prosoma width of females and males, male tuft area and leg length), duration of first copulation (if mating occurred), date of egg sac production and number of eggs produced. A preliminary analysis revealed that male prosoma width, tuft size and leg length were highly inter-correlated (Pearson correlations: prosoma width*tuft area, $r = 0.723$, $P < 0.001$; prosoma width*leg length, $r = 0.713$, $P < 0.001$; tuft area*leg length, $r = 0.729$, $P < 0.001$). As intercorrelation of so many independent variables violates a basic assumption of multiple-factor regression models, we chose prosoma width for male size measurement in all subsequent analyses, and scaled male tuft size relative to prosoma width. We used stepwise logistic regression analyses (Hardy & Field 1998) to test the effects of these variables on the: (1) probability of mating with the first male; (2) probability of re-mating; and (3) probability of cannibalism, as in Singer & Riechert (1995). We present the significance level of predictors at the point when they were eliminated from the stepwise regression. Final models only contain significant predictors, thereby providing the most economic combination of initial predictors (Hardy & Field 1998). We also present 'lack of fit' ('LOF') statistics, which test for inappropriate model form. A significant LOF indicates an inappropriate model form. We also used multiple stepwise linear regression analyses to test the effect of the variables on (1) copulation duration; and (2) the number of eggs produced.

RESULTS

Of the 101 females tested, 83 (82%) mated with the first male with which they were paired (Table 1). The probability of a female mating the first time was not significantly influenced by female size, male size, male relative tuft size or male age, but decreased significantly with female age (Table 2). Of the 18 males that failed to mate, three were cannibalized by the female. Of the 83 males that did mate, 12 were cannibalized by the female after mating. Damage to the cannibalized males made accurate measurement impossible and so further analysis of these data was not possible. These rates of cannibalism are similar to results of another study (Persons & Uetz, unpub. data).

Copulations lasted 80–550 minutes ($n = 84$, median = 155 min) and were not normally distributed (Shapiro-Wilk test, W = 0.813, P

Table 1.—Mating and re-mating frequencies of female and male *S. ocreata*.

	n	Mate (%)	Not
Virgin females:	101	83 (82.18)	18
Previously-mated females:			
1) after 1 day	27	3 (11.11)	24
2) after 3 days	24	2 (8.33)	22
3) after 30 days:			
w/egg sac	16	0 (0.0)	16
no sac	16	0 (0.0)	16
Pooled	83	5 (6.02)	78
Virgin males:	64	49 (76.56)	15
Previously mated males:	31	20 (64.52)	11

Table 2.—Results of stepwise logistic regression elimination analysis of the probability of virgin female *S. ocreata* mating with the first male.

Variables	df	χ²	P
Eliminated predictors			
Female size	1	0.095	0.758
Male tuft size	1	0.447	0.506
Male size	1	1.242	0.265
Male age	1	2.440	0.118
Final model			
Female age	1	8.400	0.004
Lack-of-fit	28	31.643	0.326

< 0.001). The duration of copulation (ln transformed) was not significantly influenced by male age ($F < 0.001$, $P = 0.995$), male size ($F = 0.305$, $P = 0.583$), female age ($F = 0.002$, $P = 0.965$), or female size ($F = 1.043$, $P = 0.310$).

Most females mated only once; only a small percentage (7%) of females mated twice (Table 1). The data from the re-mating treatments (1 d, 3 d and 30 d) were analyzed with a contingency test, which revealed no significant difference between mating treatments ($X^2 = 3.89$, $P < 0.284$), and provided justification for pooling the data (Table 1). Results from the McNemar's chi-square test of pooled data showed a highly significant difference in the proportion of virgins and mated females accepting males ($X^2 = 51.429$, $P < 0.001$). In contrast, all males observed ($n = 95$) appeared to court and attempt mating with every female encountered (virgin and mated). Of males paired only once ($n = 64$), a majority (76.56%) successfully mated (Table 1). For those males paired with more than one virgin female ($n = 31$), almost two-thirds (64.5%) mated more than once (Table 1).

The probability of a female re-mating did not vary with treatment, size or relative tuft size of her first mate, her size or age, or second male tuft size, but did increase with the size of the second male (Table 3). Three of the five females that re-mated did not show receptivity displays before being mounted, as is usually the case (Montgomery 1903; Scheffer et al. 1996). All of these re-mated females had shown receptivity displays before accepting their first mate.

Of the five females that re-mated, none

cannibalized the male after mating. Of the 78 females that refused to mate a second time, seven (8%) cannibalized the male. The probability that the female cannibalized the male was not influenced by the second male's age, the second male's size, latency between first and second male encounters or female size, but did increase with age of the female at her first mating (Table 4).

Of the 83 females that mated, 50 (60.2%) produced egg sacs, similar to previous observations (Stratton & Uetz 1983; Uetz, unpubl.). Number of eggs produced ranged from zero (no developed eggs) to 82 ($n = 50$, mean = 37.78, SD = 18.59) and was normally distributed (Shapiro-Wilk test, W = 0.978, $P = 0.653$). The number of eggs in the egg sac was not related to female age, male size, whether the female had mated once or twice or age of first mate but approached a significant positive relationship with female size (Table 5).

Table 3.—Results of stepwise logistic regression analysis of the probability of previously-mated female *S. ocreata* mating a second time.

Variables	df	χ²	P
Eliminated predictors			
Size of first mate	1	0.088	0.766
Tuft size of first mate	1	0.145	0.703
Male age	1	0.043	0.836
Male tuft size	1	0.088	0.766
Female age	1	0.334	0.563
Female size	1	1.486	0.222
Final model			
Male size	1	5.414	0.027
Lack-of-fit	45	38.498	0.742

Table 4.—Results of stepwise logistic regression analysis of the probability of a previously-mated female *S. ocreata* cannibalizing the second male.

Variables	df	χ^2	P
Eliminated predictors			
Second male age	1	0.001	0.989
Second male size	1	0.180	0.671
Latency between first and second male encounters	1	0.570	0.450
Female size	1	0.856	0.355
Final model			
Female age at first mating	1	4.620	0.032
Lack-of-fit	21	13.97	0.871

DISCUSSION

While more data are needed on the potential for multiple mating in the field, this laboratory study has demonstrated that female *S. ocreata* appear to be essentially monandrous. Males, on the other hand, are capable of mating multiple times, and are potentially polygynous. Sexual conflict over multiple mating may therefore be inevitable, given differences in the reproductive investment by each of the sexes (Trivers 1972). If a female receives enough sperm from a single copulation to fertilize her eggs, there may be no motivation for a female to mate a second time. Additionally, mating may be a costly activity for females since copulation duration is relatively long, and could lead to loss of foraging opportunities and possibly increased risk of predation and parasite transmission (Scheffer 1992). Females would therefore be expected to exercise a higher degree of mate discrimination than males, and there is some evidence that females of this species exhibit mate choice (McClintock & Uetz 1996; Uetz & Smith 1999; Uetz 2000). However, because males

Table 5.—Results of linear regression analysis of the relationship between number of eggs and female and male independent variables.

Variables	df	F	P
Eliminated predictors			
Female age	1	0.032	0.859
Male size	1	0.378	0.543
Female mated more than once	1	0.543	0.466
Female age at first mating	1	1.170	0.287
Final model			
Female size	1	3.630	0.063

have so much to gain from additional matings, selection would favor mating with highly-resistant previously-mated females, even if it is against the female's interests.

There is some evidence in spiders that females may be able to improve the proportion of surviving offspring by choosing a high-quality mate, or by mating with multiple males (Watson 1998). On the other hand, if females are primarily monandrous, males will fertilize most or all of the eggs of each female they copulate with. Female *S. ocreata* most often produce a single egg sac with 30–50 eggs (additional egg sacs are sometimes produced; Uetz persl. obs.), which for the sake of argument might represent an estimate of maximum lifetime reproductive potential. As a consequence, for every female mated, male reproductive potential grows by an amount equivalent to that female's entire reproductive potential, as suggested by Bateman (1948). However, as this species appears to have a 1:1 sex ratio (based on results of lab rearing studies and adult population surveys in the field during the breeding season; Uetz unpubl. data), it then follows that for every male that mates more than once, others will fail to mate at all, or perhaps be cannibalized in the attempt. Variation among females in reproductive success may or may not be smaller than that among males (Bateman 1948; Arnold & Duvall 1994; Lorch 2002); however from a functional perspective this does not make it any less important.

Female monandry would be expected to select for a high degree of choosiness, but in this study 83% of females mated with randomly paired males, and the only significant predictor of mating probability was female

age post-maturity. This result may seem paradoxical, given previous studies of female choice in *S. ocreata* (McClintock & Uetz 1996; Uetz 2000; Uetz & Roberts 2002), but might be explained by several possibilities. This was a "no choice" experiment in laboratory containers where females received both visual and vibratory cues from male courtship. These conditions are unlikely in the field, and females exercising mate choice based on male traits like tuft size or courtship vigor could easily avoid further contact with less favored males. Additionally, as these spiders were collected as sub-adults and maintained under laboratory conditions for several weeks, it is probable that laboratory-housed males were in better condition than their counterparts in the field. Even so, female discrimination based on male characteristics not measured in this study cannot be excluded. In any case, these findings suggest that if the male meets some threshold criterion and a female is physiologically ready, mating will most likely occur.

If mating a second time is not in the best interest of the female, selection would favor resistance and/or avoidance of mating attempts by males, leading to a mating system with female monandry. Water striders provide an example in which sexual selection on mating behavior and morphology is a result of females seeking to avoid matings that may be costly in terms of predation risk or energy expenditure (Rowe et al. 1994; Arnqvist 1997). The importance of coercive matings in a variety of groups, especially arachnids and insects, is becoming increasing clear (Choe & Crespi 1997). While it was not possible to collect accurate data on male copulation attempts for our entire dataset, there is evidence that at least some males may attempt to force reluctant females to copulate. Although our sample size is small, results of the re-mating analysis revealed that second male size was the only significant predictor of mating with a mated female. Of the five previously-mated females that mated a second time, three did not show receptivity displays, and mated only after males "pinned" them down. Male size was a significant predictor in the analysis, suggesting that the largest males may use size to their advantage in mating with resistant females.

It is also possible that reduction in female receptivity after mating is the result of some form of chemically-mediated mechanism on the part of one sex or the other, although this explanation remains highly speculative at this time. There are studies in spiders and other arthropods documenting male manipulation of female reproductive behavior through seminal product transfer during copulation (Riemann et al. 1967; Chapman et al. 1995; Eberhard & Cordero 1995). Males that successfully render a female unreceptive to other males will have fitness benefits through exclusive paternity. This could be considered a form of "post-copulatory mate guarding", and might be mediated by male seminal fluids interacting with the physiology of the female reproductive tract (Eberhard & Cordero 1995). Additionally, since *S. ocreata* are entelegyne spiders, the first male to copulate with a female may be the principal sire of the offspring produced. Testing male preferences between mated and virgin females may give some insight into whether or not males prefer virgin females and/or actively avoid mated females. An alternative might be that mated females produce an 'anti-aphrodisiac', like the compound produced by mated female *Drosophila* to advertise their status and thereby avoid male courtship (Scott & Jackson 1990). Such an adaptation may be advantageous if male courtship decreased the amount of time a female can spend feeding or if male displays attract predators. Since all the males in this study appeared to court, this possibility seems doubtful, but given that males did not have the opportunity to escape, courtship may be a 'last ditch' effort to avoid cannibalism.

In most species, there appears to be some conflict between the sexes over the outcome of mating events (Brown et al. 1997), and results of this study indicate that potential for conflict in *Schizocosa ocreata* wolf spiders as well. While much is yet to be learned about the reproductive biology of *S. ocreata*, results presented here suggest that female monandry and male polygyny, characteristics of only a few spider mating systems studied so far (Eberhard 1985, 1996; Elgar 1998), may apply to this species. These results must be interpreted with caution, however, as they represent outcomes of laboratory studies in simple enclosed containers, and conditions are obviously different in the complex leaf litter environment of the natural habitat. Even so, confirmation of assumed mating systems will

allow more robust predictions in future studies of mate choice.

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